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ON MATE CHOICE IN TWO XEROPHILIC SPECIES OF LAND SNAILS, *BREPHULOPSIS CYLINDRICA* (PULMONATA, ENIDAE) AND *XEROPICTA DERBENTINA* (PULMONATA, HYGROMIIDAE)

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On Mate Choice in two Xerophilic Species of Land Snails, *Brephulopsis cylindrica* (Pulmonata, Enidae) and *Xeropicta derbentina* (Pulmonata, Hygromiidae). Kramarenko, S. S., Kramarenko, A. S. — The cases of assortative mating are known in varied species of Gastropoda, however it is unclear how widely distributed this reproductive strategy is across the class. The data concerning land snails (Stylommatophora) are especially contradictory. By using two model species of stylommatophoran mollusks, *Brephulopsis cylindrica* (Menke, 1828) and *Xeropicta derbentina* (Krynicki, 1836), we conducted a long-term observation of their copulatory behavior in Southern Ukraine. In *X. derbentina*, a clear pattern of the positive assortative mating with respect to body size was found, whereas assortative mating in relation to shell banding polymorphism was revealed in 2 cases out of 7. *B. cylindrica* snails copulate with any available mate partner, regardless of its size.
Key words: mate choice, assortative mating, Gastropoda, *Brephulopsis cylindrica*, *Xeropicta derbentina*.

Introduction

Brephulopsis cylindrica (Menke, 1828) is a xerophilic species of land snails widely distributed in the Crimea as well as in the northern coastal areas of the Azov and Black Seas (Vychalkovskaya, 2008; Balashov et al., 2013; Balashov, 2016). It inhabits mostly dry open biotopes and demonstrates a high tendency to sinantropization: the snails were found in urbanized habitats of Lvov (Sverlova, 1998), Kyiv (Vychalkovskaya & Kramarenko, 2008), Brest (Rabchuk & Zemoglyadchuk, 2011), Chișinău (Balashov et al., 2013 a) and Belgorod (Snegin et al., 2017).

Xeropicta derbentina (Krynicki, 1836), another species of land snails, has similar ecological requirements, but its range is much wider as compared to the former species: *X. derbentina* occurs in Libya, Turkey to eastern Bulgaria, eastern Romania, southern Ukraine (including Crimea), Caucasus, France, Italy (Welter-Schultes, 2012; De Mattia, Pešić, 2014; Balashov, 2016). The species has also been recorded from Moldova (Balashov et al., 2013 a) and Russian Federation (Adamova et al., 2018). In Ukraine, the synantropic colonies of this snail have been recorded from settlements of the Poltava, Vinnitsa, and Zakarpattia Regions (Gural-Sverlova, Gural, 2017); the findings of *X. derbentina* made outside of settlements are known chiefly from the coastal zone lying south from 47° N.

The two aforementioned species are characterized by a high ability to expand their range; this may be explained by high plasticity of their life cycles (Kramarenko, 1997; Kiss et al., 2005). Both *B. cylindrica* and *X. derbentina* have a great reproductive potential with similar quantitative characteristics (Kramarenko, 2002, 2013; Vychalkovskaya & Kramarenko, 2006). In addition to their capability for active dispersal (Popov, Kramarenko, 2004; Vychalkovskaya & Kramarenko, 2006 a), both species demonstrate abilities for passive dispersal, mostly by means of anthropochory (Aubry et al., 2006; Kramarenko, 2014; Gural-Sverlova, Gural, 2017).

However, despite the fact that the reproductive biology of the two species is well studied, the mechanisms of mate choice, in relation to either shell size or to shell phenotype, are almost unknown in both species.

The term *assortative mating* (AM) denotes situations when interbreeding individuals are phenotypically rather similar but the choice of a mating partner is nonrandom and the phenotypes across mate pairs are correlated, either positively or negatively (Jiang et al., 2013). The choice of partners may depend on various features, either qualitative or quantitative (e. g. body size). Detecting the presence and causes of AM is important because this mating pattern is usually accompanied by sexual selection and thus may have a profound impact on the genetics and demographics of animal populations (Crespi, 1989).

Though there is a wealth of records or studies concerned with assortative mating in terrestrial snails, these data remain rather contradictory. In most cases, a random pattern of mating, in respect of both body size and shell colouration (banding pattern) has been reported (Wolda, 1963; Baur, 1992), although there are studies which proved the reality of assortative pairing in this group (Johnson, 1982; Asami et al., 1998; Kimura et al., 2015). Theoretically, the potential adaptive significance of AM for terrestrial gastropods is obvious, since the choice of a larger mate would enhance the reproductive success of hermaphroditic animals. In land snails and slugs, the 'female' fecundity (number of clutches, clutch size, and egg size) usually positively correlates with the shell size (Wolda, 1963; Peake, 1978; Baur, Raboud, 1988; Baur, Baur, 1998).

Ridley (1983) suggested that the three conditions are needed for the emergence of AM in natural populations: 1) the correlation between sizes of males and their success in reproductive competition; 2) the correlation between sizes of females and their fecundity; 3) the prolonged period of copulation. In addition, the size-dependent AM should take place in hermaphroditic animals with reciprocal fertilization and size-dependent female fecundity. Ridley (1983) argued that in this situation all individuals evenly contribute to reproduction (give all their eggs), and, consequently, a discriminative selection of sexual partners should emerge. Therefore we predict that land snails should prefer to copulate with the mating partner of as large size as possible.

The main aim of this study was to investigate the mechanisms, which control the selectivity in mate choice, on the basis of the results of our long-term field observations on copulation in two species of land gastropods in Southern Ukraine.

Material and methods

Species

Our field observations have been conducted in Mykolayiv City, southern Ukraine, between 1995 and 2008. Two common species of terrestrial snails, *B. cylindrica* (family Enidae), and *X. derbentina* (family Hygromiidae), were studied. The detailed characteristics of sampling sites are given in table 1. We searched for copulating pairs of the two species during seasons of their intensive reproduction — in August–September (*X. derbentina*) and May (*B. cylindrica*). In total, 1338 copulating pairs of *X. derbentina* and 170 pairs of *B. cylindrica* were registered.

The shell sizes of each individual of all copulating pairs have been measured. We used shell height (SH) and shell width (SW) in *B. cylindrica*, and the greater diameter (GD) in *X. derbentina* as the proxies of their shell sizes. Besides, in 1996, shells of *X. derbentina* from 'Namyv' population (see table 1) were measured following a more complicated scheme (Sverlova et al., 2006), including additional measurements such as

Table 1. The sampling sites of the two snail species used in this study

Population	Species	Biotope*	Sampling years	Coordinates
MNAU	*Brephulopsis cylindrica*	A lawn in the Mykolayiv National Agrarian University campus	2004, 2008	46.967 N 31.959 E
Mykolayivska		A waste ground near Mykolayivska street	2002	46.941 N 32.047 E
Namyv	*Xeropicta derbentina*	A lawn near the Mykolayiv Regional Hospital	1995–1999	46.955 N 31.942 E
UTZ		A waste ground near the Pivdenna Turbine Plant	1998–1999	46.935 N 32.053 E

*All sampling sites situated in Mykolayiv City, southern Ukraine.

the lesser diameter (LD), SH, aperture height (AH), and aperture width (AW). The whorls number (WN) of these shells was also counted. All measurements were carried out by means of the ocular-micrometer of a stereoscopic microscope, with accuracy to the nearest 0.05 mm (the whorls number was counted with precision to 0.1 whorls).

X. derbentina snails were additionally divided into two phenotypic classes in respect of their shell-banding polymorphism: B — specimens with banded shells and UB — unbanded specimens.

Statistical analysis

The null-hypothesis was that both studied species select their sexual partners randomly, i. e. there is no size-assortative mating. To test it, we applied three different approaches. The first one was based on the one-way ANOVA, where the sizes of individuals from the copulating pairs were used as the dependent variable, whereas pair-number was the explanatory variable. If shell sizes of individuals within the copulating are similar but sizes of snails from different pairs differ from each other (i. e. size-assortative mating is observed), the calculated value of the F statistic will exceed its critical value for the degrees of freedom number $df_1 = n-1$ и $df_2 = n$ (n — the number of copulating pairs analyzed). A similar approach was used by Vreys & Michiels (1997) in their study of size-dependent mating behavior in hermaphroditic flatworms.

The second method is based on the Pearson's correlation coefficient (r_p) between shell sizes of individuals from copulating pairs. However, since it is impossible to determine for the hermaphroditic organisms the size of which individual should be regarded as a dependent variable (Y) and which, as an independent (X), we used a nonparametric approach to assess the level of significance of the obtained estimate r_p. First, we calculated r_p for individuals randomly distributed between groups X and Y. Next, for a half of individuals, we changed their group affiliation (from X to Y or contrary), and calculated r_p for this 'pseudosample'. This procedure has been repeated 99 times. The mean and its standard deviation (SD) were calculated for the 100 pseudoestimates of r_p. If snails choose their partners depending on their body size, then the value of r_p will exceed its critical value for the degrees of freedom number $df = n-2$.

The third approach exploits the nonparametric permutation test (p_{perm}). We calculated the absolute difference between shell sizes of individuals from each copulating pair. The sum of these differences for all pairs was used as a criterion (K):

$$K = \sum_{i=1}^{n} \left| T_{1i} - T_{2i} \right|, \quad (1)$$

where T_{1i}, T_{2i} — size of the first and second individual of the i-th pair of n pairs used in analyses.

Next, the first individuals from each pair have been randomly permuted, and a new pseudoestimate of the K_p criterion was obtained. This procedure has been repeated 999 times. The p_{perm} estimate was calculated as a number of cases when the K_p pseudoestimate was less or equal to K, divided by 1000 (Shitikov et al., 2008).

A similar approach, with using of bootstrap resampling techniques, has been used in a study of size-assortative mating in hermaphroditic intertidal limpets (Pal et al., 2006).

The null-hypothesis of randomness in mating partner choice with respect to shell-banding polymorphism in *X. derbentina* was tested by means of comparison of the empirical and predicted (theoretical) frequencies of copulating pairs consisting of snails of the same or contrasting phenotypes (B-B, B-UB, UB-UB). The G-test (Sokal, Rohlf, 1995) was used for this end.

All statistical tests were performed with STATISTICA (StatSoft Inc.) and MS Excel for Windows.

Results

Of the seven observations of *X. derbentina*, which were used to test the hypothesis of nonselectivity in the choice of the mating partner, the null hypothesis was confirmed in five cases (table 2). In two instances ('Namyv' population, 1998 and 'UTZ' population, 1999), a significant non-random pattern of formation of copulating pairs was detected (G-test: in both cases $p < 0.05$). In both cases, there was an excess of pairs consisting of individuals with the same banding pattern (BB or UB-UB) and, correspondingly, a deficiency of pairs made up of individuals with different shell phenotypes (B-UB). Thus, in this case, one can speak of the positive assortativity in the choice of a sexual partner by *X. derbentina* based on the pattern of shell banding.

The null-hypothesis of the randomness of the mating partner choice by *X. derbentina* in relation to shell size was rejected in all cases and with using all three different methodological approaches (table 3). Moreover, in some cases, the level of significance (when testing the hypothesis about the deviation from zero of the calculated estimates of the variances ratio and Pearson's correlation coefficient) reaches the level of 10^{-8}–10^{-14}. The higher values of significance levels obtained using the permutation criterion (at the level of 0.001–0.003)

Table 2. Test of the hypothesis of random formation of copulating pairs in *Xeropicta derbentina* with respect to shell banding pattern

Population / year	n[1]	$p \pm SEp$[2]	Phenotypes in a copulating pair[3]			G-test[4]
			B-B	B-UB	UB-UB	
Namyv / 1995	73	0.86 ± 0.03	52 53.5	21 18.0	0 1.5	1.81
Namyv / 1996	71	0.77 ± 0.04	41 42.6	28 24.8	2 3.6	1.15
Namyv / 1997	149	0.97 ± 0.01	140 140.2	9 8.7	0 0.1	0.22
Namyv / 1998	193	0.90 ± 0.02	159 155.9	28 34.2	5 1.9	**4.82**
Namyv / 1999	393	0.94 ± 0.01	347 346.5	44 45.0	2 1.5	0.20
UTZ / 1998	100	0.46 ± 0.05	26 21.2	40 49.7	34 29.1	3.82
UTZ / 1999	358	0.72 ± 0.02	207 185.0	102 144.0	49 28.0	**28.76**

[1]n — number of copulating pairs studied; [2] — frequency of banded snails and its statistical error; [3] — above lines — the actual frequencies; below lines — the expected frequencies calculated under that assumption that mating is random; [4] — significant values of the G-test are in bold ($p < 0.05$).

are explained, chiefly, by the relatively small number of permutations used in the analysis (only 999 times).

Thus, the reality of size-assortative copulation in studied populations of the *X. derbentina* snails has been proved: the individuals with larger shells prefer to mate with conspecifics of similar shell size and, on the contrary, very rarely they choose a smaller individual as a sexual partner.

However, the strength of this pattern in *X. derbentina* was found to depend upon a shell trait used as a proxy for body size (table 4). The highest expression of AM is observed when GD or LD was used as a proxy, whereas the using of SH, AH, and AW revealed only a weak albeit still significant correlation between shell sizes of copulating snails. On the contrary, we failed to detect AM with respect to whorls number in *X. derbentina*. The null-hypothesis was not rejected by using the Pearson's correlation coefficient ($p = 0.06582$),

Table 3. Test of the hypothesis of random formation of copulating pairs of *X. derbentina* with respect to the shell great diameter

Population / year	n[1]	ANOVA		Pearson's r[2]		Permutation criterion (p_{perm})[3]
		F (df_1; df_2)	p	$r_p \pm SD$	p	
Namyv / 1995	73	2.43 (72; 73)	0.00010	0.419 ± 0.008	0.00023	0.001
Namyv / 1996	71	2.34 (70; 71)	0.00022	0.404 ± 0.009	0.00047	0.001
Namyv / 1997	149	1.76 (148; 149)	0.00032	0.276 ± 0.004	0.00065	0.001
Namyv / 1998	193	2.21 (192; 193)	$3.1 \cdot 10^{-8}$	0.377 ± 0.003	$6.7 \cdot 10^{-8}$	0.001
Namyv / 1999	393	2.15 (392; 393)	$3.4 \cdot 10^{-14}$	0.366 ± 0.002	$7.0 \cdot 10^{-14}$	0.001
UTZ / 1998	100	1.79 (99; 100)	0.00193	0.285 ± 0.005	0.00405	0.003
UTZ / 1999	358	1.48 (357; 358)	0.00011	0.194 ± 0.002	0.00022	0.001

[1]n — number of copulating pairs studied; [2] — for 100 random permutations of individuals within copulating pairs; [3] — for 999 random permutations of individuals between copulating pairs.

Table 4. Test of the hypothesis of random mating in *X. derbentina* (1996, 'Namyv population) with respect to various shell traits

Shell trait	ANOVA		Pearson's r[1]		Permutation criterion (p_{perm})[2]
	F	p	$r_p \pm SD$	p	
GD	2.34	0.00022	0.404 ± 0.009	0.00047	0.001
LD	2.41	0.00015	0.417 ± 0.011	0.00030	0.001
SH	1.88	0.00444	0.308 ± 0.011	0.00891	0.021
WN	1.55	0.03328	0.220 ± 0.011	0.06582	0.011
AH	1.72	0.01202	0.267 ± 0.012	0.02425	0.010
AW	1.86	0.00493	0.304 ± 0.010	0.01006	0.005

[1] — for 100 random permutations of individuals within copulating pairs; [2] — for 999 random permutations between copulating pairs.

and the one-way ANOVA returned values of p close to the minimum significance level (p = 0.03328). We may explain it by a rather weak correlation between the absolute shell size (GD) and WN (r_p = 0.588). In other words, there are specimens with a large shell but with low WN, and vice versa. For example, the size (GD) of shells with 4.8 whorls varied from 9.9 to 15.1 mm, whereas individuals with GD equal to 13.3 mm had shells consisting of 4.6 to 5.25 whorls (fig. 1).

As concerns another species of land snails investigated by us, *B. cylindrica*, we failed to find any evidence of AM in two populations studied during this work. The null-hypothesis of the random choice of the mating partner in respect of shell size was confirmed irrespectively of which measure, SH or SW, was chosen (table 5). In this case, the significance levels of the calculated statistical criteria were more or less close for all three methods used, especially for ANOVA and the nonparametric permutation criterion. It means that the *B. cylindrica* snails copulate with any available partner, regardless of its shell size. However, we have to note that in one population ('MNAU', 2008), we obtained two (out of 100) estimates of r_p (0.235 and 0.247) with $p \leq 0.05$ when analyzed mate choice selectivity in respect of shell width. Thus, under certain circumstances and using only this method, we could come to wrong conclusions about the presence/absence of AM in *B. cylindrica* of this population.

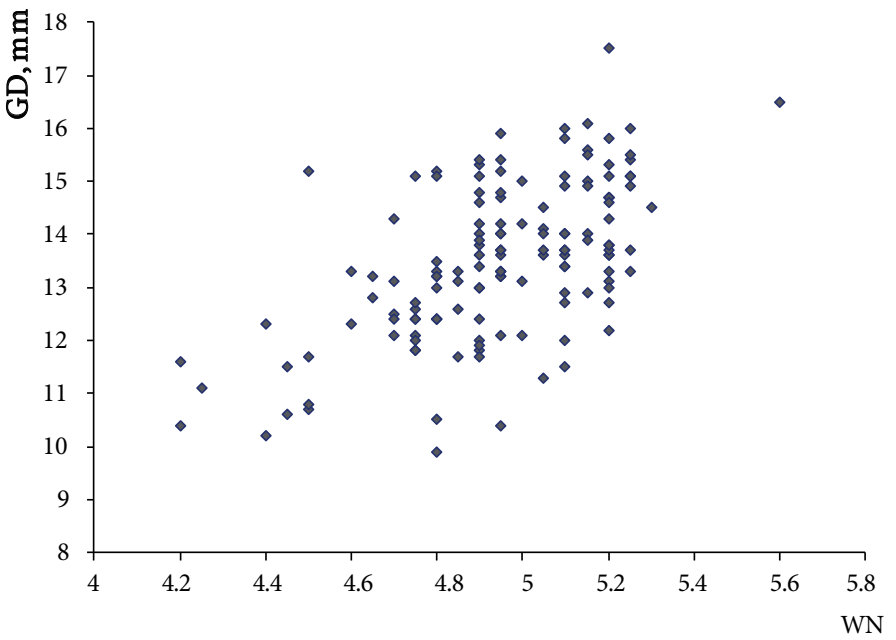

Fig. 1. The relationship between GD and WN in shells of *Xeropicta derbentina* ('Namyv' population, 1996).

Table 5. Test of the hypothesis of absence of size-assortative mating in *Brephulopsis cylindrica*

Population / shell trait / year	n^1	ANOVA		Pearson's r^2		Permutation criterion (p_{perm})[3]
		F (df_1; df_2)	p	$r_p \pm SD$	p	
MNAU / SH / 2004	50	0.73 (49; 50)	0.860	–0.155 ± 0.013	0.284	0.694[4]
MNAU / SW / 2004	50	0.95 (49; 50)	0.575	–0.028 ± 0.015	0.848	0.472[4]
MNAU / SH / 2008	70	1.32 (69; 70)	0.123	0.140 ± 0.012	0.331	0.104
MNAU / SW / 2008	70	1.48 (69; 70)	0.053	0.194 ± 0.010	0.177	0.101
Mykolayivska / SH / 2002	50	0.86 (49; 50)	0.707	–0.078 ± 0.015	0.592	0.818
Mykolayivska / SW / 2002	50	0.70 (49; 50)	0.893	–0.177 ± 0.015	0.218	0.806

[1] n — number of copulating pairs studied; [2] — for 100 random permutations of individuals within copulating pairs; [3] — for 999 random permutations of individuals between copulating pairs; [4] — for 499 random permutations of individuals between copulating pairs.

Discussion

In two studied snail species, the contrasting results were obtained: *X. derbentina* seems to use shell size as a cue for mate choice, whereas *B. cylindrica* demonstrates the randomness in partner choice. The analysis of the literary data indicates that there is no a pattern common for all terrestrial gastropods. For example, in such species as *Arianta arbustorum* and *Helix pomatia*, no signs of non-randomness in mate choice were observed (Baur, 1992). The same was true for the succineid snail *Succinea putris* (Jordaens et al., 2005). The known cases of positive size-assortative copulation in land gastropods include the bradybaenid *Bradybaena pellucida* (Kimura et al., 2015) and the slug *Veronicella sloanii* (Clarke, Fields, 2013). We wish to note that the three cases of random mating cited above represents laboratory experiments, when the snails were offered a limited set of potential sexual partners, with shells of varied size. Under natural conditions, the assortment of potential partners must be much wider.

The estimates of the strength of assortment between copulating pairs varied significantly in different populations and in different years within the same population. For instance, in 'Namyv' population of *X. derbentina*, the values of the Pearson's r_p varied from 0.276 in 1997 to 0.419 in 1995. In another population of the same species ('UTZ'), studied in 1998 and 1999, the values of r_p were essentially lower (0.194–0.276). In all these cases, the non-random partner choice in respect of shell size (greater diameter) was detected.

As concerns *B.cylindrica*, we failed to observe the non-random copulation in two populations studied (see table 5). However, according to data of Vychalkovskaya (2011), in another population of this species, also located in Mykolayiv City, AM takes place and the strength of assortativity is significant ($p < 0.001$).

Similar observations were made on gastropods of other taxa. For example, in the marine opisthobranch *Aplysia californica* the correlation between body masses of the copulating individuals in 1985 was 0.240 (Pearson's r_p; $p = 0.098$), whereas in 1986 the value of this coefficient dropped to 0.007 ($p = 0.910$) (Pennings, 1991). A strong difference in the Pearson's r_p values among geographically distant populations was found in another marine snail, *Littorina littorea*. It was 0.528 ($p < 0.001$) among pairs collected on the western shore of the Saltö Island (Sweden), whereas the same value for the pairs collected on the eastern shore of this island constituted only 0.147 ($p = 0.520$) (Erlandsson, Johannesson, 1994).

Rolan-Alvarez et al. (2015) and Ng et al. (2016) have examined a phenomenon dubbed by these authors SCE (*the scale-of-choice effect*). Using the marine gastropods of the genus *Echinolittorina* as a model object, they demonstrated that the pooling of individual sam-

ples into a single heterogeneous sample may produce bias in the Pearson's r_p values. The prerequisite for SCE is that the shell sizes within a population are much more similar than between samples.

In the two cases studied by us (*B. cylindrica* and *X. derbentina*), the sizes of observation plots did not exceed 100 meters, and no internal barriers, which could subdivide the populations, were found. Therefore, we do not expect that SCE could bias our data.

The assessments of the strength of the size-assortative mating depend on which conchiometric variables are used as "proxies" for the shell size. For example, in the 'Namyv' population of *X. derbentina*, studied by us in 1996, the values of r_p varied from 0.220 (when the whorls number was used as a proxy) to 0.417 (the lesser diameter served as a proxy). Besides, in the first case the estimate was insignificant ($p > 0.05$), though the uses of other shell characters allowed us to reject the hypothesis of random copulation (see table 4).

A similar situation was observed in a study of size-assortative mating in the nudibranch snail *Felimare zebra* (Crozier, 1918). In this species, the body lengths of the copulating partners proved to be highly correlated ($r = 0.608$; $p < 0.001$), while the use of the body volume did not give a significant relationship ($r = 0.135$; $p = 0.28$).

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